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GROWTH AND METABOLISM OF THREE INTRODUCED SUMMERSED PLANT SPECI--ETC(U)  
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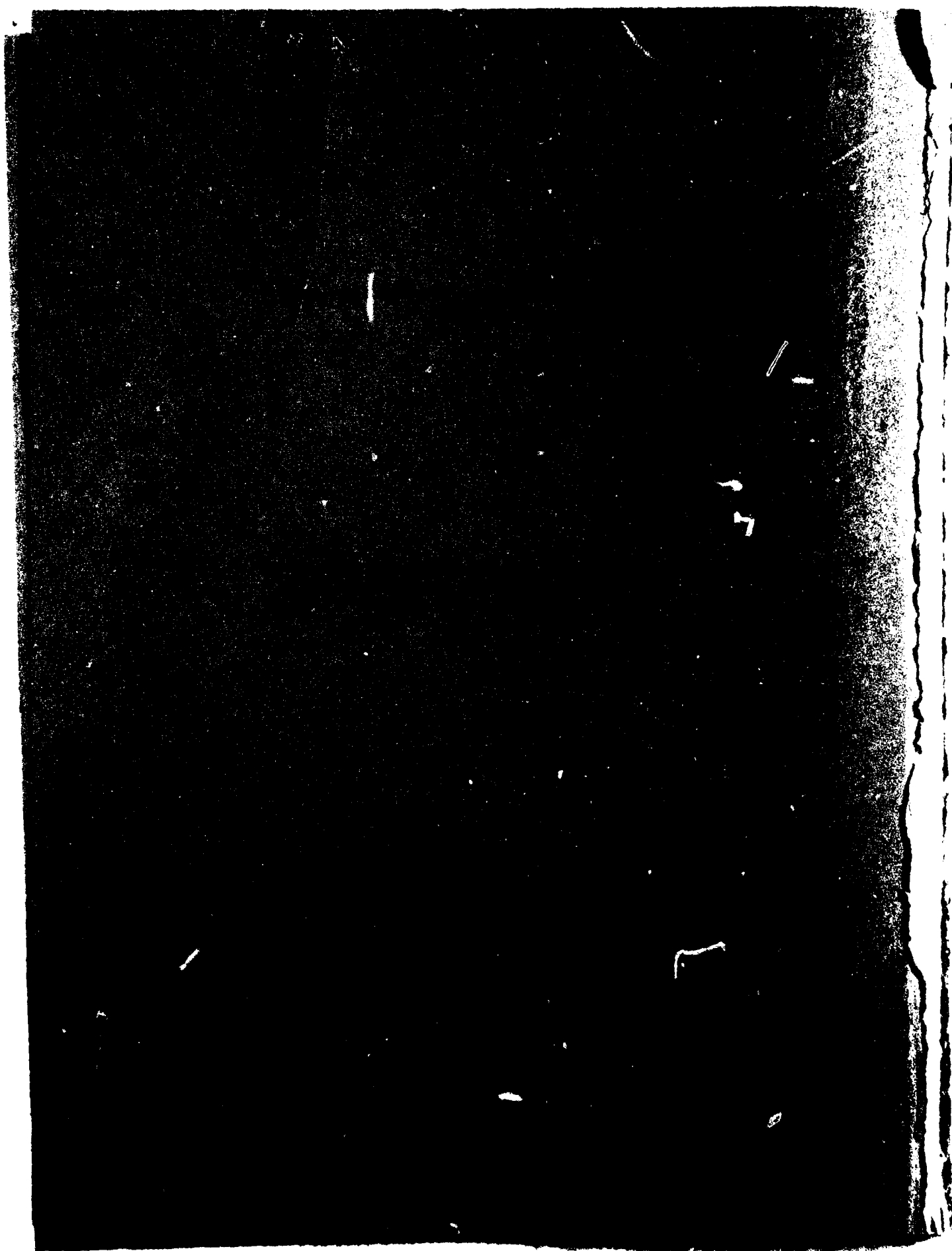
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20. ABSTRACT (Continue on reverse side if necessary and identify by block number) Under controlled experimental conditions, the influences of light and temperature on the growth and metabolism of <i>Egeria densa</i> Planch, <i>Hydrilla verticillata</i> Royle, and <i>Myriophyllum spicatum</i> L. were comparatively examined. Light was controlled at six levels ranging between 5 and 75 percent of full sunlight at peak solar noon. Water temperature was controlled at five levels ranging between 16° and 32°C. Growth considerations included morphology, biomass, and nutrition. Photosynthesis, respiration, and CO <sub>2</sub> compensation points (Continued)		

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20. ABSTRACT (Continued).

were determined to evaluate physiological differences in plant growth due to the effects of temperature and light.

External morphology in these species was significantly affected by the experimental ranges of light and temperature conditions. Both low light and high temperature promoted extensive shoot elongation and associated canopy formation. Biomass production and carbon metabolism were affected more by temperature than light. Each of the species demonstrated metabolic acclimation to light over a broad range. Conversely, they were not strictly capable of acclimating to temperature, and the productivity of individual species was strongly responsive to this factor.

Growth rate and the seasonal progression of senescence were interrelated in these species. Higher temperatures stimulated growth and promoted a compression of the growth cycle. The relationship between photosynthesis and respiration (P:R) was appreciably reduced by senescence, but the  $\text{CO}_2$  compensation point did not reflect this condition. In the species examined,  $\text{CO}_2$  compensation points decreased with increasing temperature, suggesting adaptations to low free  $\text{CO}_2$  levels in the environment. ←

The seasonal progression of growth and the geographical distribution of these species appear to be strongly influenced by integral seasonal temperature. Light is probably the primary determinant of their depth distribution, but its importance in this regard may be somewhat diminished by their significant abilities to extend to the water surface under low light conditions.

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## PREFACE

This investigation was supported by the Aquatic Plant Control Research Program (APCRP), sponsored by the Office, Chief of Engineers, and managed by the U. S. Army Engineer Waterways Experiment Station (WES), Vicksburg, Miss.

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The Commanders and Directors of the WES during the study and preparation of the report were COL J. L. Cannon, CE, and COL N. P. Conover, CE. Technical Director was Mr. F. R. Brown.

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GROWTH AND METABOLISM OF THREE INTRODUCED SUBMERSED  
PLANT SPECIES IN RELATION TO THE INFLUENCES  
OF TEMPERATURE AND LIGHT

PART I: INTRODUCTION

1. Nutrition may be of secondary importance to other environmental factors controlling the growth of submersed macrophytes in many aquatic systems. Most rooted macrophytes are able to obtain nutrients from the sediment as well as from the water (Denny 1972; Barko and Smart 1981), and may thereby be quite effective in satisfying their nutritional requirements. Indeed, nutritional investigations have demonstrated a lack of nutrient limitation of submersed macrophytes in moderately eutrophic systems (Peltier and Welch 1970, Carpenter and Adams 1977, Peverly 1980). In these types of systems, light availability may be reduced by abiotic turbidity, high densities of phytoplankton (Jupp and Spence 1977), and epiphytic algae (Phillips, Eminson, and Moss 1978). Thus, the depth distribution of macrophytes may often be limited by the availability of light (Spence 1967, 1972, 1976).

2. Investigations of the comparative light relations of submersed macrophytes have demonstrated differing degrees of physiological tolerance to shade (Spence and Chrystal 1970a; Haller and Sutton 1975; Titus and Adams 1979a). Moreover, morphological variations in some species have been experimentally induced by modifying light conditions (Spence 1976, Spence and Dale 1978). Shade tolerance and light-related morphological changes may confer competitive advantages in light-limiting situations, thereby influencing macrophyte community composition. For this reason, it is necessary to evaluate the comparative light requirements and tolerances of different submersed macrophyte species.

3. In macrophyte-dominated lacustrine systems, vertical profiles of light and water temperature in the littoral zone roughly parallel one another (Dale and Gillespie 1977; Bowes, Holaday, and Haller 1979). Moreover, seasonal changes in photoperiod and incident solar radiation



correspond with substantial changes in water temperature in nearly all aquatic systems. Thus, the effects of light on the growth of submersed macrophytes in nature may be linked with the influence of temperature in this regard.

4. In lakes of relatively high water clarity, temperature may act in concert with hydrostatic pressure in limiting the depth distribution of submersed macrophytes. For example, Sheldon and Boylen (1977) reported the occurrence of *Elodea canadensis* Michx, a vascular macrophyte, to a depth of 12 m in Lake George, New York. This depth reportedly corresponded with the "base of the thermocline" and exceeded by approximately 2 m the maximum depth of colonization based on hydrostatic pressure considerations (discussed in Wetzel (1975) and Hutchinson (1975)).

5. The influence of water temperature on the geographical distribution of macrophytes is essentially unknown. Contrary to the assertion of Sculthorpe (1967) that temperature does not fundamentally control the distribution of macrophyte species, there are some indications based on geographical distribution data (Sculthorpe 1967, Holmquist 1971) and on seasonal growth data (Rich, Wetzel, and Thuy 1971; Boylen and Sheldon 1976; Haag and Gorham 1977) that different macrophyte species possess different and discrete ranges of thermal tolerance. These differences may affect competitive relations among species. Temperature may also influence seasonal growth cycles and delimit the latitudinal range of macrophyte species.

6. In a continuing experimental effort involving the examination of various environmental factors on the growth of submersed macrophytes, we have investigated the introduced species, *Egeria densa* Planch, *Hydrilla verticillata* Royle, and *Myriophyllum spicatum* L., which have demonstrated a significant ability to displace native aquatic vegetation in North America. Our nutritional studies have confirmed the ability of these species to utilize sediment nutrients, and quantified their potential role in sediment phosphorus cycling in lacustrine systems (Barko and Smart 1980). Here we report the results of an investigation designed to comparatively assess the influences of light and temperature on the growth and metabolism of these same species. Growth considerations

include morphology, biomass, and nutrition. Metabolic responses (photosynthesis, respiration, and  $\text{CO}_2$  compensation) to light and temperature are examined to evaluate the physiological basis for observed differences in growth. The distribution of individual macrophyte species is largely dependent upon their specific breadth of adaptability, i.e. ability to grow under different environmental conditions. Thus, we apply the results of this investigation in examining various aspects of the distribution of the submersed macrophytes considered herein.

## PART II: MATERIALS AND METHODS

### Experimental Environment

7. The investigation was conducted during the months of June and July 1979 in white fiberglass tanks contained in the greenhouse facility of the Environmental Laboratory, U. S. Army Engineer Waterways Experiment Station (WES), Vicksburg, Miss. The 18 tanks used in the study were positioned into six groups of 3 tanks interconnected by short lengths of 7.6-cm inside diameter (ID) flexible plastic tubing. Each tank measured 150 x 90 x 90 cm deep and was filled with deionized (reverse osmosis) water to a depth of 83 cm, thus providing a volume of ca. 1200 l per tank and an interconnected volume of ca. 3600 l per group. Water was continuously circulated among the tanks in each group by a pair of liquid circulators (Remcor Corp. Model CFF 500, Chicago, Ill.), providing complete hydraulic exchange about every 1.5 hr. Circulating units were equipped with heating and cooling systems and a two-stage thermostat, which allowed the maintenance of selected water temperatures with less than a 1°C diel fluctuation. Water temperatures ranged from 16° to 32° in 4°C increments, with an additional 24°C category, and were randomly assigned to each of the six groups of tanks.

8. Six light (shade) levels were provided through the use of neutrally absorptive polypropylene shade fabrics of variable mesh density (Chicopee Co., Cornelia, Ga.) manufactured to fit over clear lucite covers conforming to the areal dimensions of the tanks. Experimental shade levels (Figure 1) ranged from 0 to 93 percent with 0 shade representing a lucite cover with no shade fabric. Corresponding PAR\* (LICOR-quantum sensor determinations) ranged from peak solar noon values of ca. 100  $\mu\text{einsteins}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$  at 93 percent shade to 1500  $\mu\text{einsteins}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$  with no shade, representative of 5 to 75 percent of full sunlight at this latitude. Light determinations were made at middepth in the center of tanks and were somewhat affected by shading from the sides, as

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\* PAR = photosynthetically active radiation.

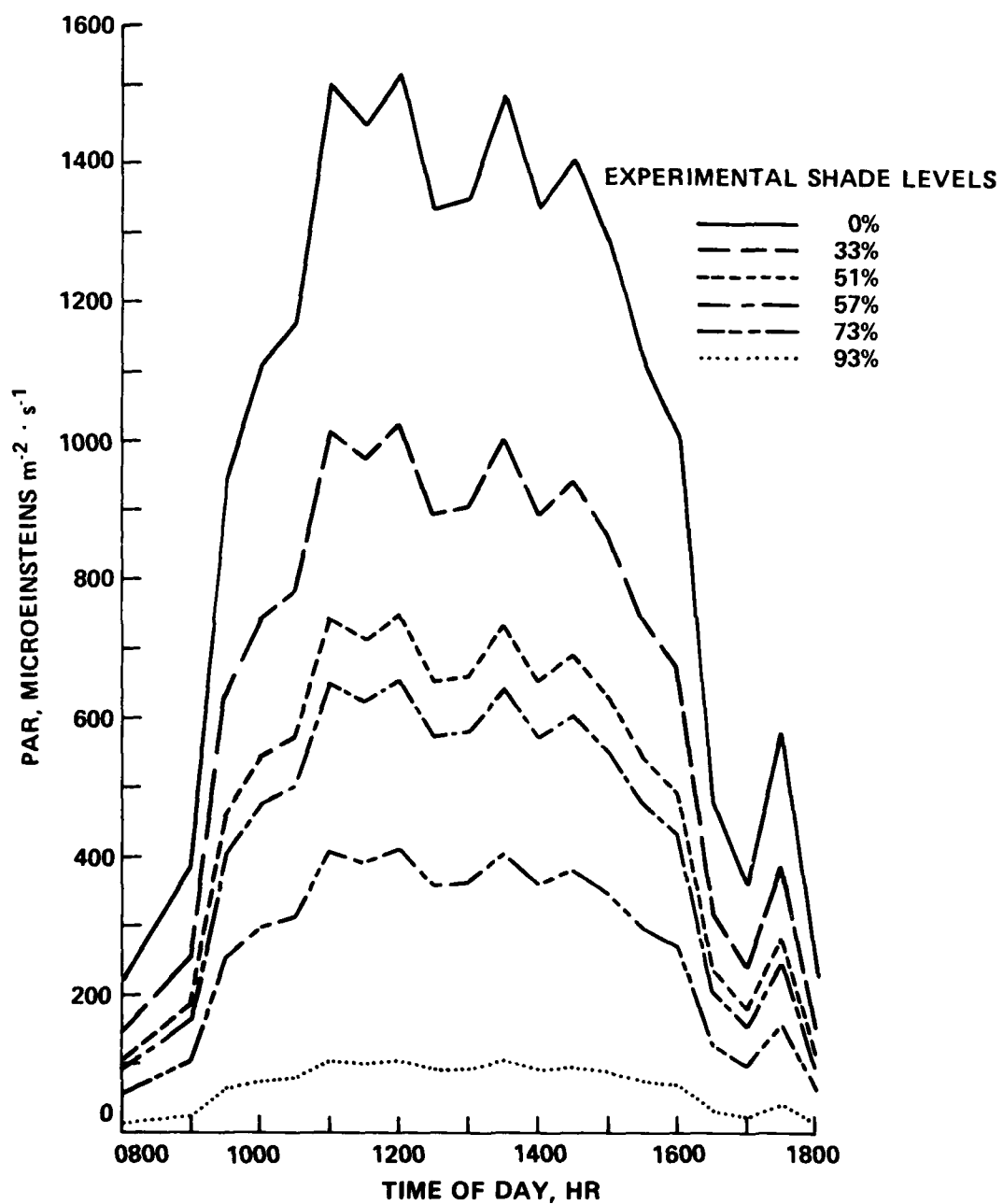


Figure 1. Experimental shade levels and associated diel irradiance

apparent in the truncated and erratic light levels observed in the early morning and late evening (Figure 1).

9. Within the main body of the study, intermediate shade levels of 33, 57, and 73 percent were randomly assigned to tanks in each group of three. Shade levels of 0, 51, and 93 percent were randomly assigned to the three remaining tanks in the additional 24°C temperature group. This allowed examination of the influence of a much greater range of light conditions on plant growth under intermediate thermal conditions.

10. The chemical composition of the solution in which the plants were grown is characterized in Table 1. We purposely excluded most major nutrients from solution in order to minimize algal growth during the investigation. Our experience has indicated optimal growth of many rooted submersed macrophyte species on a variety of sediments in this simple solution.

11. The sediment used in this study was obtained from a sublittoral region in Lake Washington, Wash.; it was predominantly fine textured, containing ca. 20 percent sand, 75 percent silt, and 5 percent clay by dry mass. Nutrient composition of the sediment (Table 1), assessed by standard analytical techniques (described in Barko and Smart 1979a), indicated optimal conditions for plant growth. This is reflected in the luxuriant growth of submersed aquatic vegetation in some sections of Lake Washington.

#### Experimental Procedures

12. The Lake Washington sediment was thoroughly mixed prior to allocating it to 432 one-litre plastic sediment containers. These containers afforded a surface area of ca. 90 cm<sup>2</sup> and a depth of ca. 14 cm. After allowing a 1-week period for the consolidation of sediment in the containers, sediment depth was adjusted to 13 cm and it was covered with a 1-cm layer of washed silica sand to minimize the introduction of suspended sediment and nutrients into the tank solution.

13. *Egeria densa* and *Hydrilla verticillata* were obtained from central Florida, and *Myriophyllum spicatum* was obtained from Lake

Table 1  
Characterization of Sediment and Solution Chemistry. Means and Standard  
Errors (Where Determined) are Based on Three Replications

Sediment Chemistry		Interstitial Water Concentrations		Solution Chemistry	
Sediment Concentrations mg·g <sup>-1</sup> dry mass		mg·l <sup>-1</sup>		Constituent*	Conc mg·l <sup>-1</sup>
Organic matter	119.4 ± 0.1	NH <sub>4</sub> -N	9.6 ± 0.0	NaHCO <sub>3</sub>	84.0 Alkalinity 0.9 meq·l <sup>-1</sup>
Total Kjeldahl nitrogen	3.9 ± 0.0	PO <sub>4</sub> -P	0.05 ± 0.02	CaCl <sub>2</sub>	66.0 Conductivity 280 μmhos·cm <sup>-1</sup> (20°C)
Total P	0.70 ± 0.02	Ca	53.0 ± 1.7	HCl	5.1 pH 7.5
Ca	7.4 ± 1.1	Mg	17.2 ± 0.4		
Mg	5.7 ± 0.3	K	5.6 ± 0.2		
K	1.3 ± 0.3				

\* Added to glass-distilled water.

\*\* Determination made 24 hr after solution preparation.

Washington. These species, hereafter referred to by their generic names, were prepared for planting by clipping 12-cm apical sections from young plant shoots maintained in shaded water baths at 24°C during the planting process. One third of the sediment containers (i.e., 144) were randomly assigned to each of the three species. All plants were placed to a sediment depth of ca. 4 cm at a density of four plants per container. Eight replicate containers per species were equally positioned as separate blocks in each of the 18 tanks. The position of each species (i.e., middle versus ends of a tank) was randomly assigned for each temperature-light combination. Shade fabrics were positioned immediately and water temperatures (held initially at 24°C) were slowly adjusted over a 2-day period to experimental levels. Continuous aeration was provided by twin air lifts uniformly delivering ca. 3.75 l air·min<sup>-1</sup> to each tank. The air was supplied by a compressor and was filtered and humidified prior to its introduction into the tanks. During the investigation, water temperatures were continuously monitored and minor thermostat adjustments made as necessary. Shade fabrics remained continuously in place.

14. The experiment was terminated after a 6-week period of growth due to the excessive deterioration of *M. spicatum* and the extensive formation of dense canopies by all species, which could have led to reduced light levels under some experimental conditions. Seven of the eight replicate containers were harvested for examination of morphology and biomass accumulation. The remaining container was maintained under the experimental conditions for later examination of metabolism.

#### Growth Determinations

##### Morphology

15. Shoot length for each container was determined as the distance from the sediment surface to the average position of the shoot apices. Shoot number was determined by counting the number of shoots in each container at a point approximately one third up the shoot length. This procedure excluded shoots formed in the canopy. Thus,

a source of bias in the data was eliminated since significant canopy production occurred only under some experimental conditions and not others. Nodal frequency was determined as the number of nodes per unit length in both upper (canopy) and lower (near sediment) portions of the shoots.

#### Biomass and nutrition

16. Shoot biomass was determined for all plant containers harvested at the end of the growth phase of the investigation. Root biomass was determined for only three of seven replicate containers per species in each tank. Roots were separated from the sediment by gentle washing over a 1-mm mesh sieve. All plant materials were weighed after drying at 80°C in a forced air oven to constant mass. After inspection of the mass data, shoots of each species were selected from minimum and maximum growth conditions (i.e. low and high biomass) for analyses of N, P, and K contents. These were ground in a Wiley mill and digested with a 30 percent hydrogen peroxide-concentrated sulfuric acid mixture, slightly modified (for differences in volume) from Allen et al. (1974). Analyses of N and P were performed with a Technicon Autoanalyzer; K analyses were determined by flame photometry using standard procedures.

#### Metabolism Determinations

17. One week after concluding the growth phase of experimentation, rates of photosynthesis and respiration and CO<sub>2</sub> compensation points in *Egeria* and *Hydrilla* shoots grown under the various conditions of temperature and light were determined. *Myriophyllum*, which was in an advanced state of deterioration at this time, was excluded from these experiments.

18. Metabolism studies were conducted in a controlled environment chamber in which CO<sub>2</sub> exchange was determined in closed systems by infrared gas analysis. Each metabolism system consisted of a glass cylinder (44 cm tall × 6.2 cm in diameter) sealed with a rubber stopper and connected by flexible plastic tubing to a tubing pump (Masterflex Corp.). Total volume approximated 1.25 l, but varied slightly among systems.



Temperature was regulated by immersion in glass water baths equipped with Remcor Corp. circulating units (as described for greenhouse application). Light was provided by Sunbrella Fixtures (Chagrin Falls, Ohio) containing a combination of Multi-Vapor and Lucalox (sodium vapor) high intensity lamps. Maximum PAR delivered at the plant surfaces was  $1050 \mu\text{einsteins}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$ , ca. 30 percent less than maximum midday values determined in the greenhouse. Light levels were varied with shade fabrics identical to those used in the greenhouse.

19. Plant shoots were prepared by gently removing as much loosely adherent inorganic and epiphytic material as possible, then cutting the shoots to a length of 30 cm (or less with shorter shoots) measured downward from the apex. Several shoots were inserted into each cylinder until a total volume of 20 to 25 ml of solution (Table 1) was displaced. Shoot mass (oven dry) averaged 1 g but varied between 0.6 and 1.4 g across species and treatments. Shoots were completely emersed in the solution as it was adjusted to a final volume of 1 l. Thus, the gas volume of each system approximated 250 ml. Air was supplied from an outside source and continuously circulated at a rate of  $800 \text{ ml}\cdot\text{min}^{-1}$  from the air space through plastic diffusers positioned near the shoot bases. Air flow gently agitated the plant leaves and prevented the accumulation of gas bubbles within the foliage.

20. In studies of light response, we simultaneously subjected shoots cultured at 0, 33, 57, 73, and 93 percent shade (and  $24^{\circ}\text{C}$ ) to the same array of shade conditions at  $24^{\circ}\text{C}$ . Because of a mechanical problem, we had to discard the data obtained for *Hydrilla*, cultured at 33 percent shade. In studies of temperature response, we separately subjected shoots cultured at  $16^{\circ}$ ,  $20^{\circ}$ ,  $24^{\circ}$ ,  $28^{\circ}$ , and  $32^{\circ}\text{C}$  (at 57 percent shade) to these respective conditions at 51 percent shade ( $515 \mu\text{einsteins}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$ ). Thus, with both light and temperature, we examined photosynthesis and respiration under conditions nearly approximating those encountered during growth. Additionally, we examined light saturation characteristics of the two species with respect to previous shade conditioning.

21. Respiration was determined first, followed by photosynthesis.

Plants were always subjected to the lowest light levels first with incrementally higher light levels used later. A minimum of 0.5 hr was allowed in reduced light and during open system exposure to the outside atmosphere between metabolism determinations in order to reestablish  $\text{CO}_2$  equilibrium between the plant, solution, and the outside atmosphere. After closing the system, samples of circulating air were removed from rubber septa every 1.5 to 3 min with duplicate 3-ml syringes for immediate  $\text{CO}_2$  analysis with a Beckman Model 865 gas analyzer and replaced with  $\text{CO}_2$ -free  $\text{N}_2$  gas to avoid pressure changes.

22. Photosynthetic depletion of  $\text{CO}_2$  was approximately linear over the first 12 to 15 min (Figure 2) with the curve becoming increasingly curvilinear as the  $\text{CO}_2$  compensation point was approached. Respiration promoted a sustained linear increase in  $\text{CO}_2$  concentration beyond our upper detection limit ( $610 \mu\text{l}\cdot\text{l}^{-1}$ ). Rates of photosynthesis and

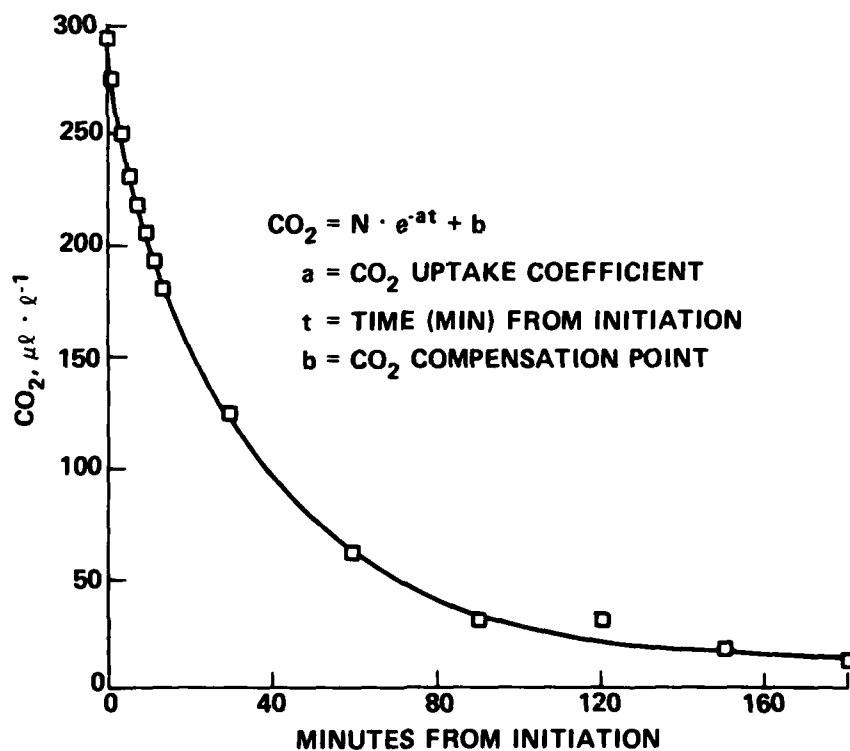


Figure 2. Photosynthetic  $\text{CO}_2$  depletion in a closed metabolism system. All determinations were made on airstream samples

respiration were estimated by linear regression analysis of data obtained during the first 12 to 15 min. Rates in most cases were based on six to eight data points, each representing an average of duplicate determinations. Carbon dioxide compensation points were estimated from  $\text{CO}_2$  depletion data obtained over a 3-hr period by a computerized, non-linear least squares approach. The equation describing the typical  $\text{CO}_2$  depletion curve presented in Figure 2 was used to provide all such estimates.

23. Rates of photosynthesis and respiration are presented on the basis of oven dry shoot mass. To what extent different leaf:stem biomass ratios may have influenced photosynthetic rate determinations among treatments is unknown. Computations account for total  $\text{CO}_2$  flux (both atmospheric and aqueous) in the systems. Aqueous fluxes were calculated from appropriate absorption coefficients at each of the temperatures. Short-term changes in inorganic carbon (other than  $\text{CO}_2$ ) were determined to be minor and were not measured. Minor differences in the volumes of the different systems, in the volumes of shoots occupying aqueous volume, and in  $\text{N}_2$  gas additions were compensated for in the calculations.

### PART III: RESULTS

#### Growth

24. With each growth response variable, a similar trend was apparent in relation to the influence of temperature at all intermediate shade levels (33 to 73 percent). Furthermore, factorial analyses of variance among the growth data for each species at the intermediate shade levels indicated that only a very minor portion of the experimental variance in any response variable could be attributed to an interaction between light and temperature. For these reasons, only main effects are considered in examining the influence of temperature on plant growth. In considering the influence of light on plant growth, comparisons are made amongst data obtained at 24°C, the only temperature level common to all shade levels.

#### Growth responses to light

25. *Hydrilla*, and to a lesser extent *Myriophyllum*, exhibited decreased shoot number with increasing shade (Figure 3). *Egeria* demonstrated depressed shoot production at high as well as at low light, with its maximal number of shoots being produced at intermediate shade levels. In contrast to the patterns observed in shoot number, both shoot length and upper to lower nodal frequency increased with increasing shade in all species (Figure 3). Under conditions of low light, these species divert their energy from the production of more shoots to the development of a canopy formed by both shoot elongation and an associated increase in the frequency of upper branches and leaf whorls. To some extent, the latter process may require a commensurate production of organic matter (biomass). For example, *Hydrilla* elongated appreciably at maximum shade, but as evidenced in its upper to lower nodal frequency, apparently did not have the organic reserves (i.e. shoot biomass, Figure 4) to effectively develop a canopy beyond the elongation stage. Although both *Egeria* and *Myriophyllum* demonstrated similar reductions in their production of organic matter at maximum shade, they were not inhibited in their ability to develop a canopy.

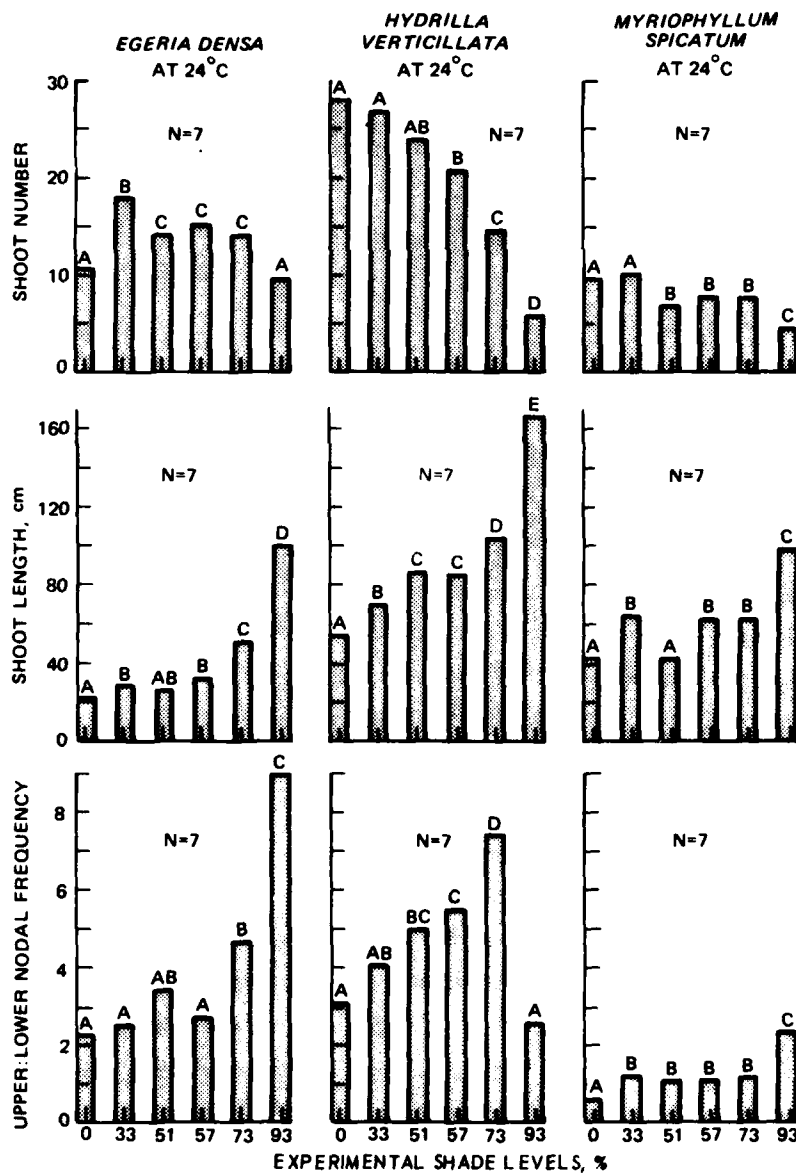


Figure 3. Morphology in relation to shade conditions. Different letters within a subfigure indicate significant differences at the 5 percent level or less based on Duncan's multiple range analysis

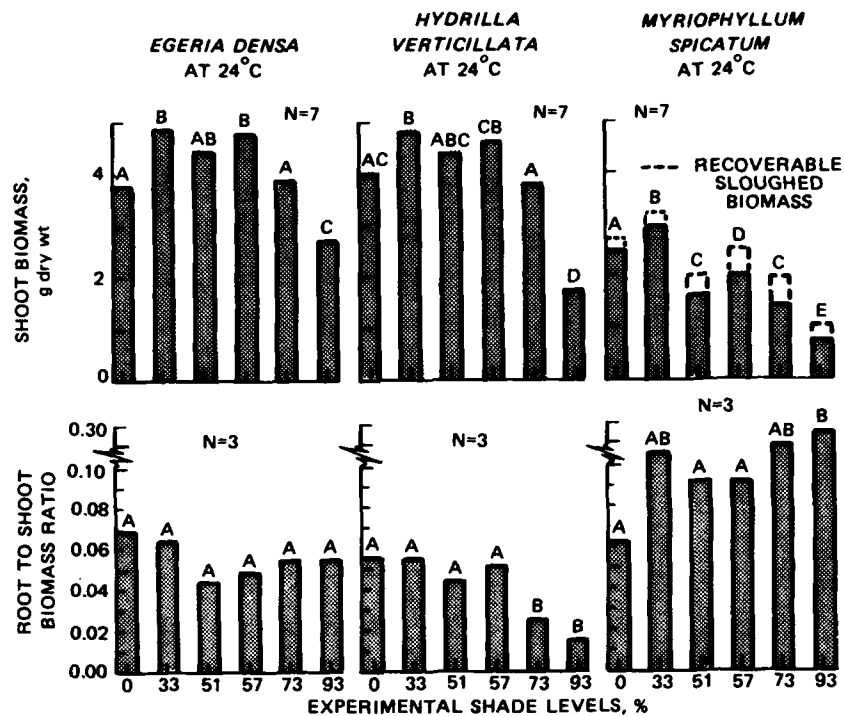


Figure 4. Biomass in relation to shade conditions. Different letters within a subfigure indicate significant differences at the 5 percent level or less based on Duncan's multiple range analysis

26. Shoot biomass profiles (Figure 4) indicate attenuated production of organic matter in all species at low light levels. Shoot biomass production was somewhat inhibited in *Egeria* and *Hydrilla* at the maximum light level as well. In these species at 24°C, negligible sloughing of biomass at any of the light levels was observed. Thus, their biomass profiles (Figure 4) are essentially representative of differences in production. In contrast, *Myriophyllum* sloughed shoot fragments considerably at 24°C, thereby obscuring the quantitative relationship between harvestable biomass and production. As indicated in Figure 4, some of these fragments were recovered during harvesting, but unknown quantities were lost through decomposition. Sloughing of shoot fragments is common in *Myriophyllum* (Grace and Wetzel 1978), and as will be discussed later, may be influenced by a variety of environmental factors. These losses, however, did not appear to be affected

by light level; thus, differences in the biomass of *Myriophyllum* are considered representative of relative differences in production in relation to light.

#### Growth responses to temperature

27. The exceptionally low values apparent in morphological attributes of the growth of *Egeria* and *Hydrilla* at 32° and 16°C, respectively (Figure 5), reflect their poor capacities for growth at these opposing extremes in temperature. *Egeria* demonstrated a slight increase, *Myriophyllum* a slight decrease, and *Hydrilla* essentially no change in shoot number with increasing temperature. This contrasts with the similar trends in shoot number demonstrated by these species in response to light (Figure 3). In all species, but to a lesser extent in *Egeria*, shoot length and upper to lower nodal frequency increased with increasing temperature.

28. Although shoot biomass in *Egeria* was not appreciably influenced by temperatures between 16° and 28°C, its biomass at 32°C was significantly reduced, indicating its intolerance to this temperature (Figure 6). Shoot biomass in *Hydrilla* (Figure 6) dramatically increased in a step-wise fashion with each 4°C increase in temperature between 16° and 32°C, which is consistent with the results Van, Haller, and Garrard (1978) reported for this species. Van, Haller, and Bowes (1976) reported an optimum temperature of 36.5°C for photosynthesis in this species. Thus, greater biomass might have been obtained at temperatures somewhat higher than the maximum temperature (32°C) provided in this investigation. At 16°C *Hydrilla* grew very poorly, but did remain metabolically active.

29. The absence of a significant trend in the shoot biomass of *Myriophyllum* in Figure 6 belies differences in its production of organic matter with temperature. Based on our observations, maximum sloughing of shoot fragments occurred at the higher temperatures, where biomass production appeared to be greater. Because of elevated rates of tissue decomposition with increasing temperature, a decreasing proportion of sloughed mass was recovered at higher temperatures at the time of harvesting. In this species, production and biomass are increasingly

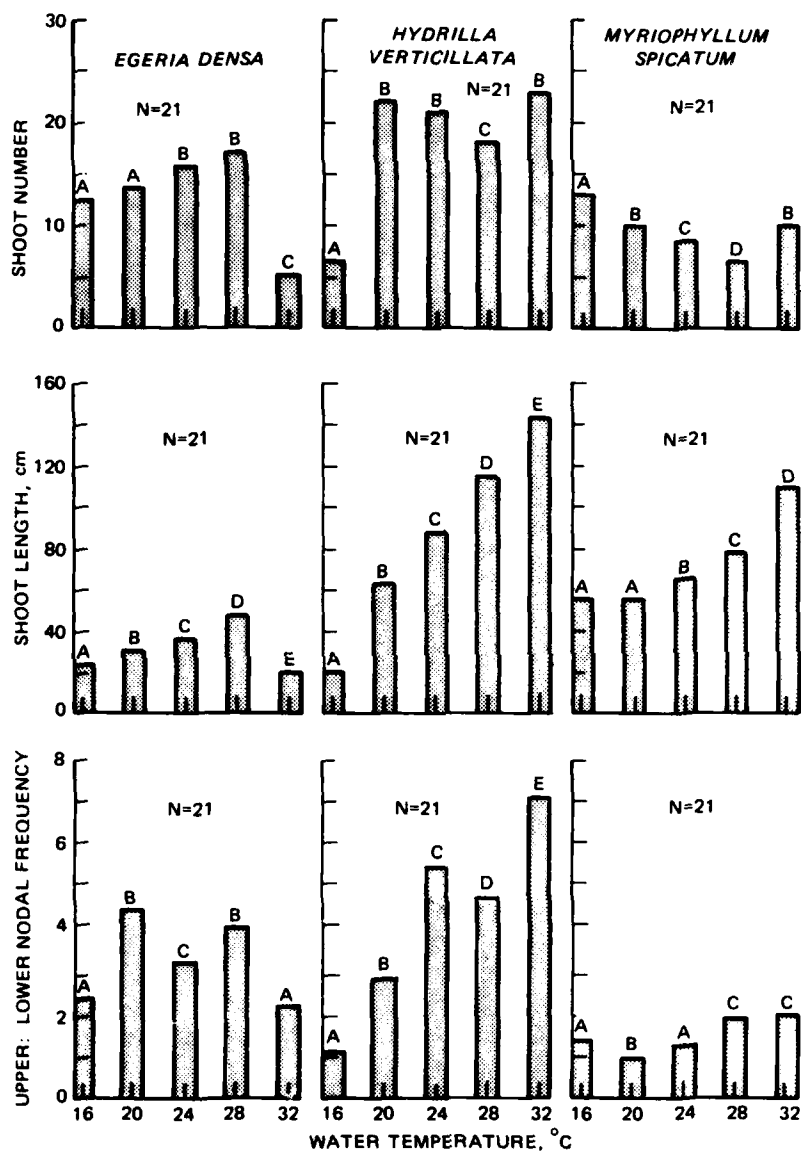


Figure 5. Morphology in relation to temperature conditions. Different letters within a subfigure indicate significant differences at the 5 percent level or less based on Duncan's multiple range analysis



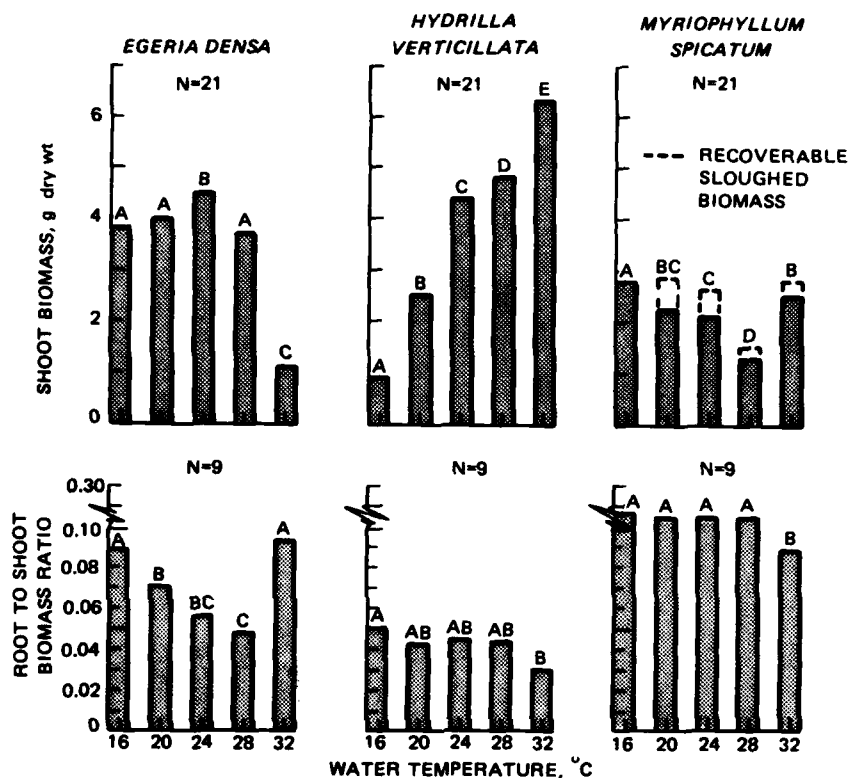


Figure 6. Biomass in relation to temperature conditions. Different letters within a subfigure indicate significant differences at the 5 percent level or less based on Duncan's multiple range analysis

unrelated at higher temperatures. This is also true of *Egeria* and *Hydrilla*, but to a much lesser extent. Root to shoot biomass ratios in *Myriophyllum* (Figures 4 and 6) exceed those in *Egeria* and *Hydrilla* at nearly all temperature and light levels, perhaps reflecting the greater losses of shoot biomass from *Myriophyllum*.

#### Nutritional considerations

30. Concentrations of N, P, and K in shoots from conditions providing minimum biomass exceeded concentrations of these elements in shoots from conditions providing maximum biomass in all species (Table 2). Dilution of nutrients in plant shoots occurred whether production was enhanced in response to either light or temperature conditions. In *Myriophyllum*, this effect was somewhat less pronounced in

Table 2  
Concentrations of N, P, and K in Plant Shoots from  
Maximum and Minimum Biomass Conditions. Means and  
Standard Errors are Based on Four Replications

Species	Nutrient Concentrations, mg·g <sup>-1</sup> dry mass					
	N		P		K	
<i>Egeria</i>						
Maximum mass	15.7	± 0.9	3.3	± 0.2	1.1	± 0.2
Minimum mass	33.0	± 0.3	4.9	± 0.2	2.7	± 0.2
<i>Hydrilla</i>						
Maximum mass	16.4	± 0.6	3.1	± 0.2	3.1	± 0.1
Minimum mass	29.6	± 0.4	6.4	± 0.1	7.2	± 0.2
<i>Myriophyllum</i>						
Maximum mass	19.0	± 0.6	5.1	± 0.2	3.0	± 0.1
Minimum mass	25.4	± 0.6	5.4	± 0.1	5.1	± 0.3

comparison with the other species because of its relatively smaller range of biomass and greater tissue sloughing.

31. Shoot N and P concentrations (Table 2) exceed the minimum requirements (i.e., critical concentrations) reported in a general sense for submersed macrophytes (Gerloff and Krombholz 1966). However, K concentrations from maximum growth conditions are low in comparison with average concentrations reported for submersed vegetation (Hutchinson 1975). Under maximum growth conditions, K concentrations in all species are less than the critical concentration of 3.5 mg·g<sup>-1</sup> dry mass established for *Myriophyllum spicatum* (Gerloff 1975). This element is apparently not readily obtainable from the sediment by submersed macrophytes (Barko and Smart 1981). Thus, K may have limited production in these species under optimal conditions of temperature and light.

## Metabolism

### Metabolism in relation to light

32. Photosynthesis in both *Egeria* (Figure 7) and *Hydrilla* (Figure 8) was incrementally greater in shoots cultured at decreasing light levels. We attribute this trend to a higher chlorophyll content and

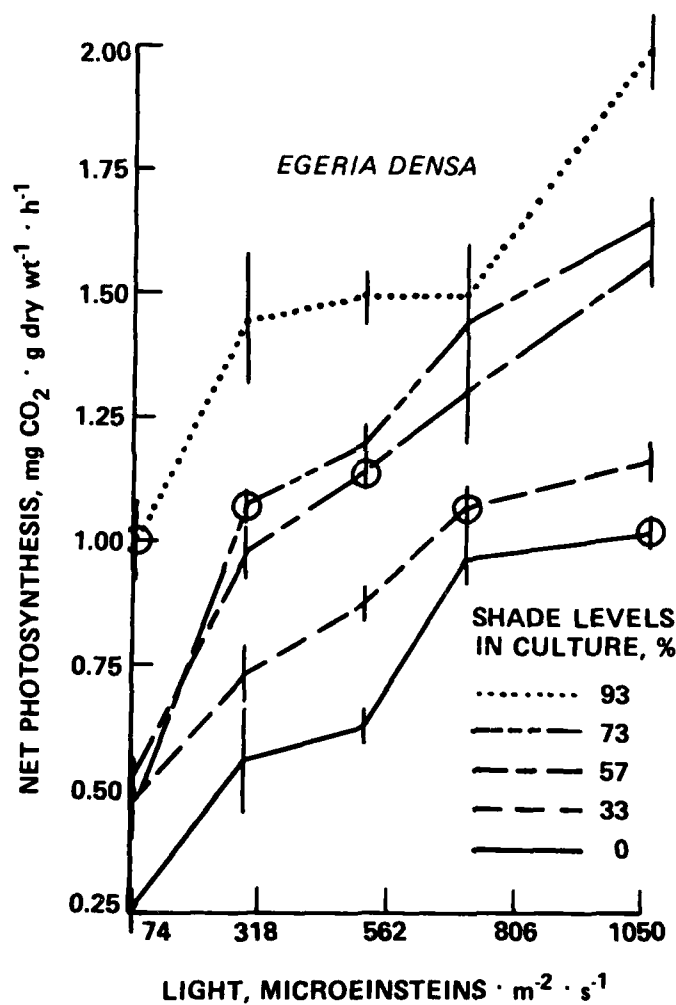


Figure 7. Photosynthesis in *Egeria* in relation to light. Rates and standard errors are based on regression estimates. Circled values represent points of approximate correspondence between light provided during experimentation and culture

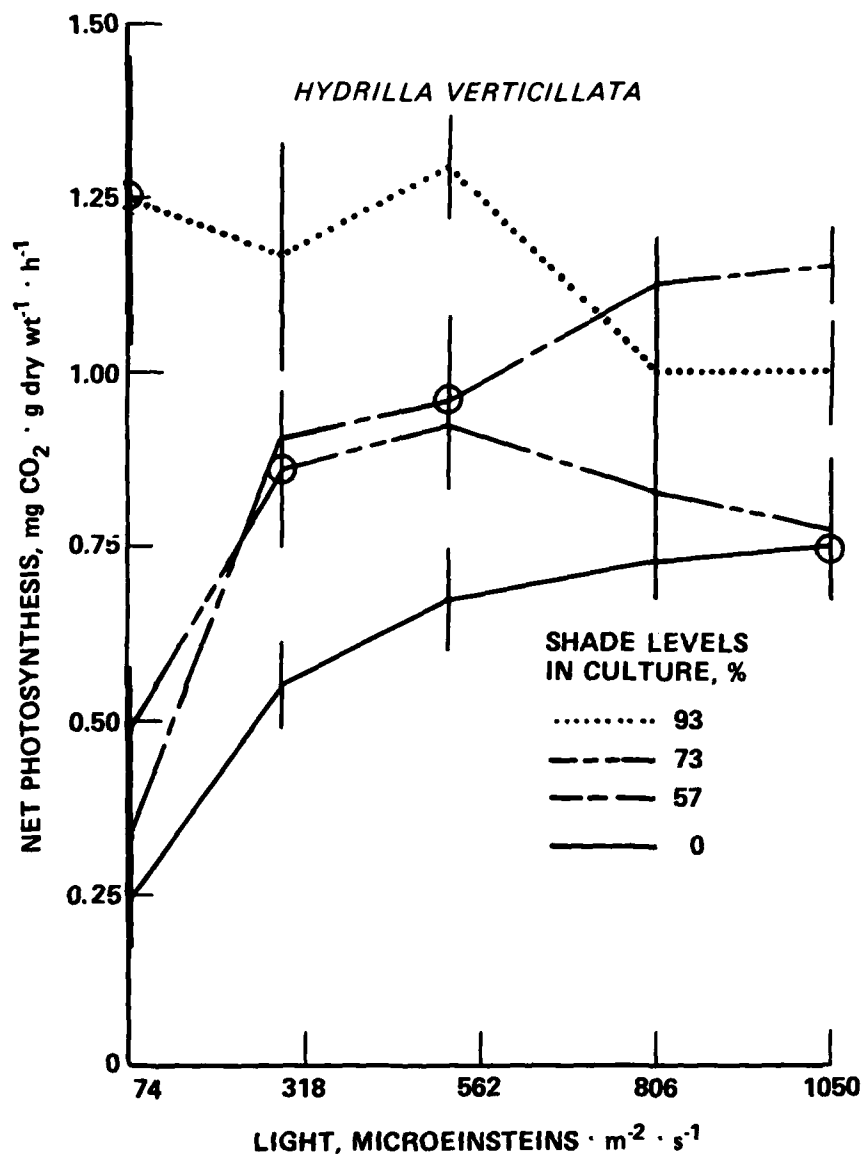


Figure 8. Photosynthesis in *Hydrilla* in relation to light. Rates and standard error bars are based on regression estimates. Circled values represent points of approximate correspondence between light provided during experimentation and culture

consequently greater assimilatory capacity in the shade-adapted shoots. Although we did not measure chlorophyll directly, differences were visually apparent. Even the stems of shade-adapted shoots were pigmented. Shade-adapted leaves of terrestrial vegetation commonly contain higher concentrations of chlorophyll than do sun leaves (Larcher 1975). The same effect has been noted in submersed macrophytes grown under conditions of low light (e.g., Bowes et al. 1977b; Wiginton and McMillan 1979). The greater photosynthetic response of the shade-adapted shoots (Figures 7 and 8) is predominantly normalized in both species when rates of photosynthesis are compared at experimental light levels approximating those provided during culture in the greenhouse. Both species are apparently able to alter their photosynthetic capacity over a broad range of available light.

33. Incrementally higher light levels (Figures 7 and 8) promoted tissue damage in shade-adapted shoots, particularly in *Hydrilla*, as evidenced by the disruption of chloroplasts and extremely chlorotic condition of the leaves at the end of experimentation. The damage to *Hydrilla* is indicated in the depressed photosynthetic response exhibited by the shade-adapted shoots at super-saturating light levels in Figure 8. *Hydrilla* is apparently more sensitive to high light (relative to conditions of preadaptation) than *Egeria*, which possesses both a greater specific leaf area and a fourfold to sixfold greater number of leaf whorls per unit stem length than *Hydrilla* (Barko, unpublished). The greater photoreceptive capacity of *Egeria* is suggested by its nearly linear photosynthetic response to increasing light irrespective of shade conditioning (Figure 7). Photosynthesis in *Hydrilla* was readily saturated at PAR values of  $1050 \mu\text{einsteins}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$  or less (Figure 8), but in *Egeria* photosynthesis was not saturated at even the highest light level (Figure 7).

34. Both *Egeria* and *Hydrilla* appear to be capable of net photosynthesis at low light levels, particularly when conditioned to low light. These species, and *Myriophyllum* as well, exhibited growth (as biomass accumulation) at diurnally variable levels of  $<100 \mu\text{einsteins}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$  in the greenhouse during an approximate 14-hr photoperiod.

Bowes et al. (1977b) reported dry weight increases in *Hydrilla* at 10 to 12  $\mu\text{einsteins}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$  during a 16-hr photoperiod. Our data suggest that *Egeria* may also be capable of growth under similar conditions.

35. Dark respiration in *Egeria* exceeded that in *Hydrilla* at all shade levels (Figure 9). Respiration was greatest in shoots of *Egeria* cultured at intermediate shade levels. In *Hydrilla*, respiration was little affected by shade preconditioning except at the 93 percent level,

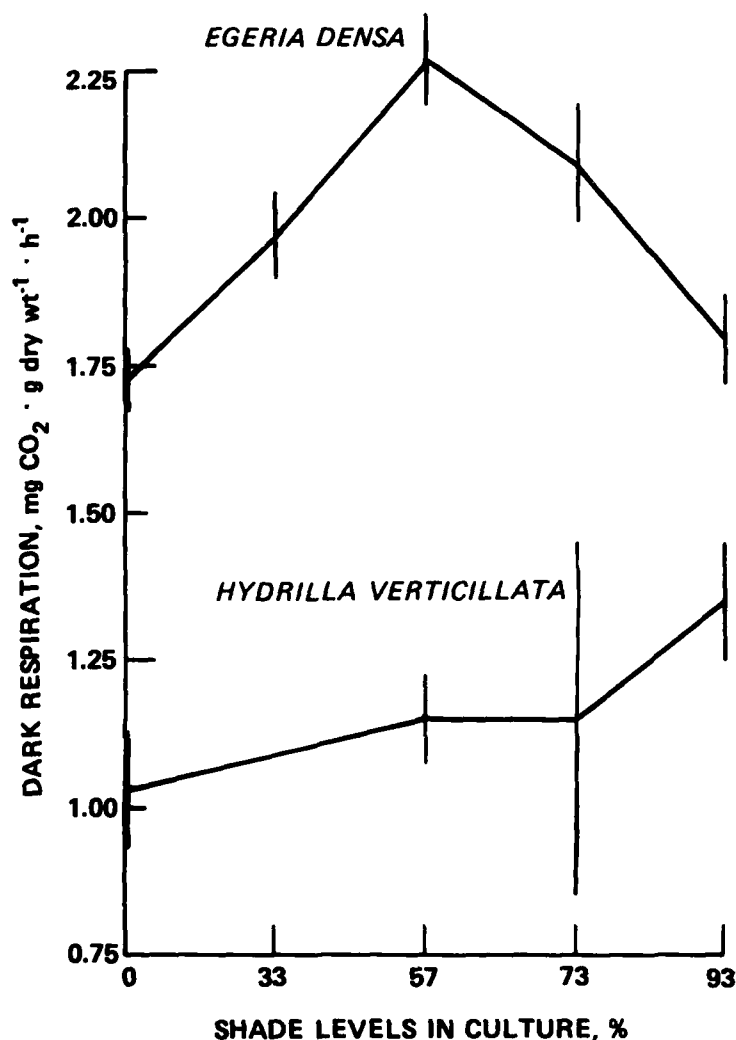


Figure 9. Dark respiration in *Egeria* and *Hydrilla*. Rates and standard errors are based on regression estimates

where it was slightly greater. With both species, the patterns observed in respiration (Figure 9) correspond with those in net photosynthesis obtained at shade levels approximating those provided during culture (Figures 7 and 8).

36. Ratios of photosynthesis to respiration (P:R) on a 24-hr basis are better related to growth (as biomass accrual) than is photosynthesis alone because the latter does not account for losses in the dark of organic matter synthesized during the day. From the low values of diel P:R in Table 3, it is apparent that both *Egeria* and *Hydrilla* at

Table 3  
Ratios of Net Photosynthesis (P) to Dark Respiration (R)  
for *Egeria densa* and *Hydrilla verticillata* in  
Relation to Shade Conditioning

Shade Level, %	P:R*	
	<i>Egeria</i>	<i>Hydrilla</i>
0	0.8	1.0
33	0.8	--
57	0.7	1.1
73	0.7	1.0
93	0.8	1.3

\* Estimated from specific metabolism data on the basis of a 24-hr day with a 14-hr photoperiod. Determinations made after a 2-month period of growth at the designated shade levels.

24°C had completed or nearly completed the growth phase of their development after ca. 2 months in this investigation. Ratios of P to R in *Egeria* are somewhat less than in *Hydrilla* because of the greater rates of respiration in the former at all shade levels. In neither species is there a definite relationship between P:R and shade conditioning; this is consistent with the results of Bowes et al. (1977b) for *Hydrilla*. However, the high P:R in *Hydrilla* at 93 percent shade (Table 3) does reflect its somewhat greater rate of photosynthesis at this level compared to other shade levels at the time of determination (Figure 8).

Metabolism in relation to temperature

37. The photosynthetic response curves for *Egeria*, and to a lesser extent *Hydrilla*, are respectively shifted somewhat toward lower and higher temperatures (Figure 10), which is consistent with trends in the biomass response of these two species. Photosynthesis in both species was more affected by temperature than by light under the conditions of this investigation. This is consistent with the greater range of biomass elicited in response to temperature compared to light conditions.

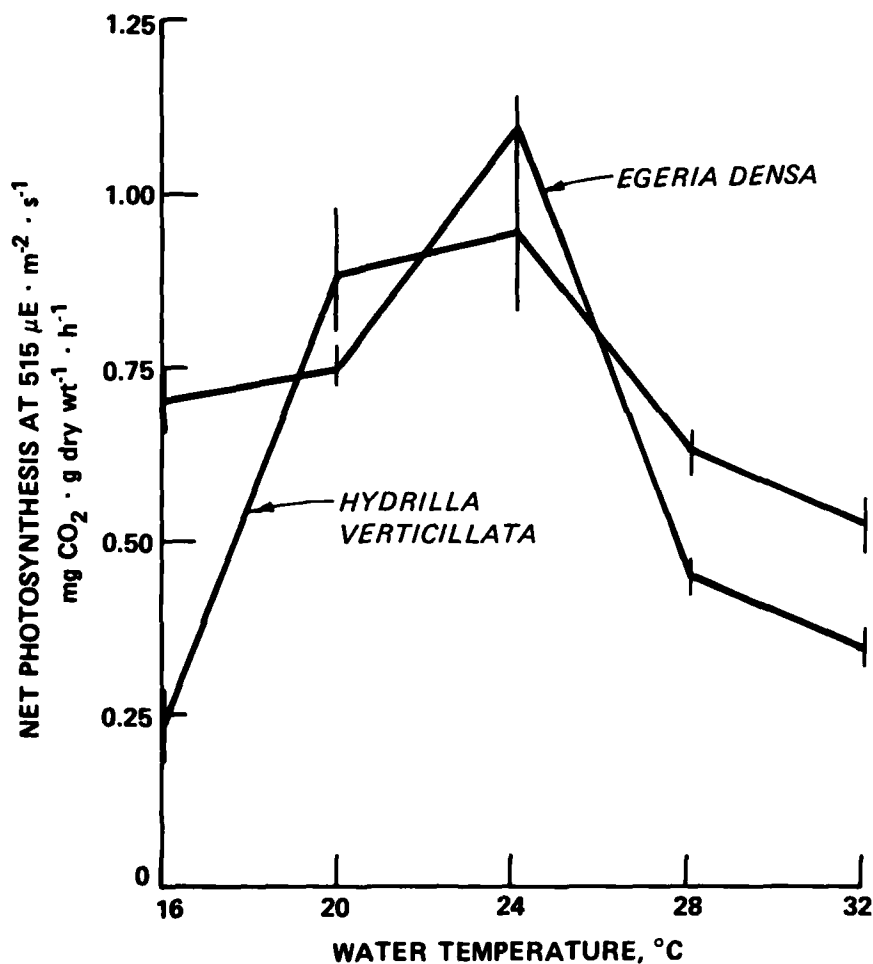


Figure 10. Photosynthesis in *Egeria* and *Hydrilla* in relation to temperature. Rates and standard errors are based on regression estimates



38. Dark respiration in *Egeria* exceeded that in *Hydrilla* at nearly all temperature levels (Figure 11). Both species demonstrated their lowest rates of respiration at 16°C. Above this temperature, respiration in *Egeria* conforms to a pattern similar to that observed in photosynthesis, with maximum rates of both processes occurring at 24°C. Respiration in *Hydrilla* above 24°C increases slightly in an inverse fashion with decreasing photosynthetic rate at higher temperatures.

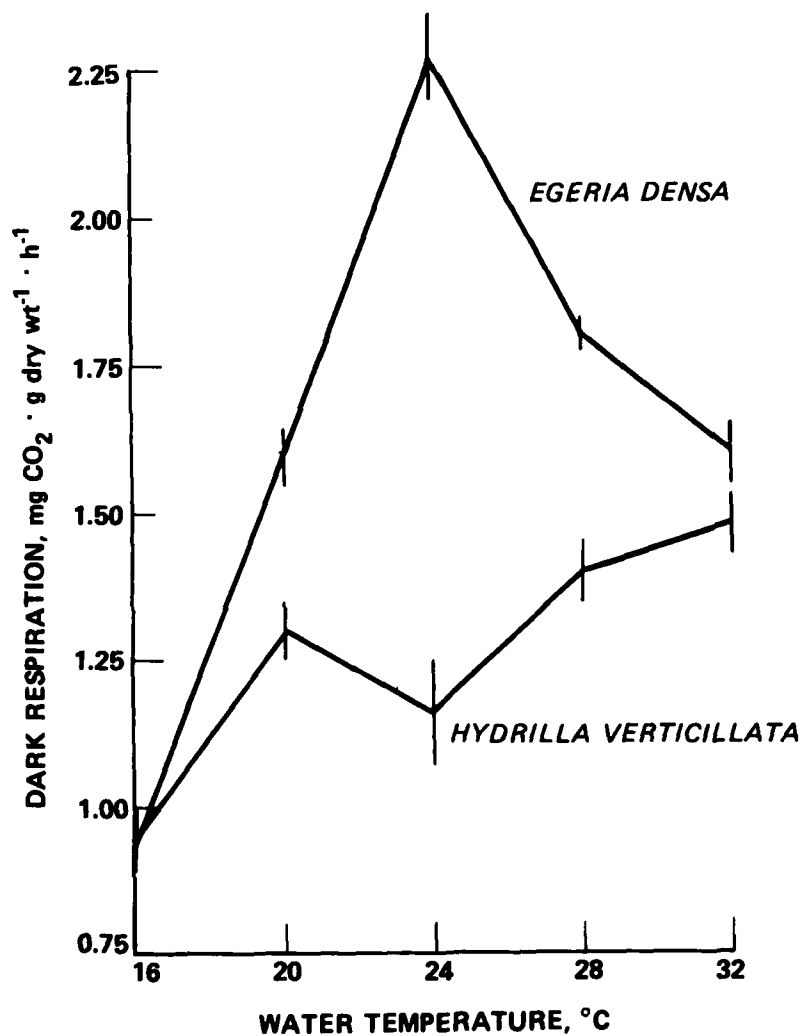


Figure 11. Dark respiration in *Egeria* and *Hydrilla* in relation to temperature. Rates and standard errors are based on regression estimates

39. The large differences in P:R exhibited by both species in relation to temperature (Table 4) contrast with the uniformity of P:R in relation to light noted earlier. The poor growth of *Egeria* at 32°C and *Hydrilla* at 16°C is respectively evidenced in their low P:R values at these temperatures. Patterns of change in P:R with temperature differ among the two species. In *Egeria*, P:R decreases with increasing temperature, but in *Hydrilla*, maximum P:R occurs between 20° and 24°C, and decreases at either extreme. With both species, P:R relationships are two temperature levels out of phase with actual biomass production. In other words, maximum P:R was determined at a level 8°C cooler than that providing maximum production of biomass.

Table 4  
Ratios of Net Photosynthesis (P) to Dark Respiration (R)  
for *Egeria densa* and *Hydrilla verticillata*  
in Relation to Temperature Conditioning

<u>Water Temperature, °C</u>	<u>P:R*</u>	
	<u><i>Egeria</i></u>	<u><i>Hydrilla</i></u>
16	1.1	0.3
20	0.7	1.0
24	0.7	1.2
28	0.4	0.6
32	0.3	0.5

\* Estimated from specific metabolism data on the basis of a 24-hr day with a 14-hr photoperiod. Determinations made after a 2-month period of growth at the designated temperature levels.

40. Compensation point data are not presented in relation to light because all values fell randomly within the 95 percent confidence intervals associated with estimates of CO<sub>2</sub> compensation point in Table 5 at 24°C. As demonstrated in the other metabolic parameters as well, the CO<sub>2</sub> compensation point in these species was affected more by temperature than light. In spite of the variability associated with our estimates,

CO<sub>2</sub> compensation points in both species generally tend to decrease with increasing temperature (Table 5).

Table 5  
Carbon Dioxide Compensation Points\* for  
*Egeria densa* and *Hydrilla verticillata*  
in Relation to Water Temperature

Temperature °C	Estimated CO <sub>2</sub> Compensation Point μl·l <sup>-1</sup> (95% C. I.)	
	<i>Egeria</i>	<i>Hydrilla</i>
16	48 (37-59)	56 (16-96)
20	25 (17-33)	20 (13-27)
24	17 (8-26)	48 (28-68)
28	20 (11-29)	39 (32-46)
32	13 (3-23)	20 (13-27)

\* Estimated from photosynthetic CO<sub>2</sub> depletion curves by nonlinear analysis of data obtained over a 180-min period. The experiments were conducted at 515 μeinsteins·m<sup>-2</sup>·sec<sup>-1</sup> and temperature levels consistent with those provided during culture.

## PART IV: DISCUSSION

### Morphological Aspects of Growth

41. Each of the three species responded similarly to decreasing light through a reduction in the numerical density of shoots, an increase in shoot length, and the associated development of a canopy. These changes represent morphological adaptations to low light, whereby photosynthetic tissues are concentrated at or near the water surface. Haller and Sutton (1975) reported a 95 percent reduction in PAR at a depth of 0.3 m beneath a dense bed of *Hydrilla* in comparison to a reduction of only 29 percent in open water at the same depth. Quantitatively similar reductions in incident radiation beneath *Myriophyllum* have been reported by Titus and Adams (1979a). In this species, canopy formation is apparently accentuated by the sloughing of leaf fragments predominantly from lower portions of the shoots. Accordingly, up to 57 percent of the biomass of *Myriophyllum* has been reported to occur within 20 cm of the water surface (Adams, Titus, and McCracken 1974). Equivalent data are not available for *Egeria*, but, on the basis of our observations, it appears similarly effective in forming a canopy.

42. The inverse relationship observed in all species between shoot length and light is supportive of the results of Spence (1976) and Spence and Dale (1978) for several species of *Potamogeton*. We are in general agreement with their observation that increasing light decreases stem elongation primarily by reducing mean internode length (i.e., increasing mean nodal frequency). However, it is important to point out that in our study the differences noted between nodal frequency in upper versus lower portions of shoots were quantitatively more significant than differences in mean nodal frequency alone. The formation of a canopy in the species considered here may be ecologically analogous to the increased specific leaf area reported in several species of *Potamogeton* in response to shade (Spence and Chrystal 1970b; Spence, Campbell, and Chrystal 1973).

43. Canopy development was stimulated by increased temperature

(within tolerance limits) as well as reduced light in our study. Again, this aspect of growth is evidenced in both the greater shoot length and increasing values of upper to lower nodal frequency. Hence, the influences of increasing temperature and light on external shoot morphology elicit opposing responses in these species.

44. In nature, the areal expansion of shoots rising rapidly to the water surface in the spring under conditions of low light may be stimulated by increasing water temperature, which could supersede or at least counteract the inhibitory influence of increasing irradiance on shoot development. Ageing has been demonstrated to gradually depress the stimulatory influence of high temperature on shoot elongation in *Potamogeton richardsonii* (A. Benn.) Rydb. during mid to late summer (Spence and Dale 1978). This effect may be applicable to the species considered herein as well. Thus, the growth cycle in terms of external morphological development in these submersed macrophytes can be hypothetically elucidated on the basis of seasonal changes in light, temperature, and endogenous ontogeny.

45. The morphological plasticity of these species is ecologically significant. Utilization of light is increased through their canopy formation, which makes it difficult for other species to effectively compete (Haller and Sutton 1975; Titus and Adams 1979a) and is probably an important factor in their adventive spread in aquatic systems. This aspect of their ecology may also be true of other canopy formers such as *Elodea canadensis* (Buscemi 1958). The morphological adaptability of these species to low light may be largely responsible for their dominance in eutrophic systems, where the growth of species demonstrating prostrate life forms (e.g. *Vallisneria*) could be relatively restricted.

#### Growth and Senescence

46. A major consequence of determining metabolic rates late in the growth cycle of these species is that our data more closely relate to senescence, the antithesis of growth, than to growth itself. Biomass production generally increased with temperature (within ranges of

tolerance) with a concomitant compression of the growth cycle.

*Myriophyllum* flowered in the intermediate and high, but not in the low temperature tanks during our study. This agrees with reported variations in the phenological development of *Myriophyllum* in nature with plants in warm water developing more rapidly than in cold water (Young 1973, Grace and Tilly 1976). Similar results have been reported for *Elodea canadensis* (Haag and Gorham 1977).

47. The influence of senescence on metabolism in *Egeria* and *Hydrilla* is apparent in their overall low rates of net photosynthesis and the low values of P:R determined after about 2 months of growth. Reduced photosynthetic rate with age has been reported in a variety of terrestrial plant species (Wilson and Cooper 1969; Osman and Milthorpe 1971; Larcher 1975). This trend is also apparent in emergent macrophytes (McNaughton 1973; Barko, Murphy, and Wetzel 1977); it has been considered in *Ceratophyllum demersum* L. (Best and Meulemans 1979) and in a variety of rooted submersed macrophytes (Haag 1979; Jana and Choudhuri 1979), and is perhaps an endogenous or environmentally induced characteristic of most vascular plants.

48. We contend that in both *Egeria* and *Hydrilla* accelerated ageing associated with higher temperatures resulted in the observed 8°C incongruity between P:R and biomass production. A similar pattern in relation to temperature was noted in whole tank metabolism determinations made approximately 2 weeks earlier (Barko, unpublished). Apparently, temperatures providing maximal growth also advanced the onset of senescence in these species. This conclusion is supported by the studies of Adams and McCracken (1974) and Titus (1977) suggesting that seasonal trends in photosynthesis correspond with changes in the physiological condition of tissues in *Myriophyllum*. In this same species, senescence occurred at least 1 month earlier in the warmer of two reservoirs studied by Stanley et al. (1976). In that study, marked differences in biomass between reservoirs (with less mass in the warmer) were attributed to differential losses of biomass during growth. The results of Grace and Tilly (1976), indicating differential ageing in *Myriophyllum* growing in different thermal regimes in a reactor cooling pond, agree with those of

Stanley et al. (1976) and also support our conclusions regarding the influence of temperature on macrophyte growth and senescence.

49. The interrelationship between growth rate and the temporal advancement of senescence reported herein in response to temperature parallels the observations of Barko and Smart (1979b) with *Myriophyllum* and *Hydrilla*, where growth rate and senescence varied with differences in substratum. In that study, macrophyte senescence on sediments providing maximum biomass production preceded the onset of senescence on sediments where minimum production occurred. It appears then that a variety of factors influencing growth rate in submersed macrophytes may affect the advancement of senescence.

50. It is possible that reduced concentrations of nutrients in tissues may be involved in the physiological decline of macrophytes subsequent to a period of rapid growth. This concept is supported by the results of Schmitt (1977) suggesting that phosphorus may limit photosynthesis in *Myriophyllum* coincident with its midsummer decline in Lake Wingra, Wisconsin. Our nutritional data implicate low potassium as a possible factor in plant senescence, and we are currently investigating this relationship in detail.

#### CO<sub>2</sub> Metabolism

51. The lack of a trend in CO<sub>2</sub> compensation point with light in *Egeria* and *Hydrilla* parallels the results of Smith, Tolbert, and Ku (1976) reported for a terrestrial species, but in the same study the authors noted an increase in CO<sub>2</sub> compensation point with increasing temperature, which is common in terrestrial plants but apparently opposes the trend observed in our study. In comparison, our results are in close agreement with those reported for *Hydrilla*, cultured at temperatures between 15° and 35°C (Bowes et al. 1977a). Since our determinations were made at various temperatures, the same as those maintained during culture, CO<sub>2</sub> compensation points could have been influenced by temperature-related differences in CO<sub>2</sub> solubility and in bicarbonate exchange equilibria, as well as by photosynthetic and respiratory processes.

However, the decrease in  $\text{CO}_2$  compensation point with increasing culture temperature reported by Bowes et al. (1977a), consistent with our findings, was determined at a constant experimental temperature and has been again demonstrated by Holaday and Bowes (1980).

52. In our study, the low  $\text{CO}_2$  compensation points at high temperatures are somewhat difficult to rationalize in view of the lower rates of photosynthesis determined at these temperatures. However, senescence (if a consequence of a nutritional deficiency or simply an endogenous consequence of growth) could have reduced overall metabolism without necessarily altering the  $\text{CO}_2$  compensation point. The results of Jana and Choudhuri (1979) indicating reductions in both photosynthesis and photorespiration with age in *Vallisneria spiralis* L. support this possibility. Alternatively, differences in internal shoot morphology, demonstrated to affect  $\text{CO}_2$  refixation in some submersed species (Sondergaard 1979; Sondergaard and Wetzel 1980), could have promoted differences in the compensation point irrespective of changes in photosynthetic potential with age. Variations in internal shoot morphology (not determined) might have been equivalent to the significant external variations noted in our study. However, the significance of  $\text{CO}_2$  refixation (or the lack thereof) in *Egeria* and *Hydrilla* has not yet unequivocally been demonstrated.

53. It must be recalled that biomass production, particularly in *Hydrilla*, did generally increase with temperature. We view the lower compensation points as evidence for an increased affinity for  $\text{CO}_2$  in the species considered herein. In our investigation, the lower  $\text{CO}_2$  compensation points may indicate adaptation to the reduced availability of free  $\text{CO}_2$  in water at higher temperatures. Free  $\text{CO}_2$  is generally considered to be the carbon source of preference in photosynthesis (Steemann Nielsen 1947; Stanley 1970; Van, Haller, and Bowes 1976). However, a strong relationship between environmental carbon supply in the bicarbonated form and the productivity of *Myriophyllum spicatum* has recently been demonstrated (Adams, Guilizzoni, and Adams 1978).

54. The environmentally related intraspecific variations in  $\text{CO}_2$  compensation point reported for several submersed macrophytes (Van,



Haller, and Bowes 1976; Bowes et al. 1977a; Holaday, Haller, and Bowes 1977; Sondergaard 1979; Bowes, Holaday, and Haller 1979) apparently reflect physiological differences related to both site and season. Holaday and Bowes (1980) have recently postulated that a low  $\text{CO}_2$  compensation point in *Hydrilla* during midsummer may indicate a physiological adaptation (involving  $\text{C}_4$  intermediates) to low daytime levels of free  $\text{CO}_2$ . Hough (1979) suggests that seasonal variations in  $\text{CO}_2$  compensation point may reflect changes in photorespiration. In our investigation, lower  $\text{O}_2$  concentrations (not determined) at high temperature levels may have contributed to reduced photorespiration rates. Whatever the causes, these variations in  $\text{CO}_2$  compensation point need to be carefully considered in any comparisons made among species.

55. Large discrepancies in compensation point estimates between gas phase and liquid phase determinations have been noted (Hough and Wetzel 1978; Sondergaard 1979). In addition to the several causes postulated by the authors cited above as resulting in these discrepancies, we emphasize that these methods potentially measure changes in somewhat different carbon pools--free  $\text{CO}_2$  in the atmospheric method and total inorganic carbon (TIC) in the aqueous method. At the point of compensation of free  $\text{CO}_2$  in our investigation, TIC concentrations continued to decline because bicarbonate and carbonate sources of carbon had not been depleted (Barko and Smart, unpublished). Thus, our compensation point data indicate the ability of these plants to reduce concentrations of free  $\text{CO}_2$ , but do not necessarily indicate their ability to compensate the entire TIC system. The ability of submersed macrophytes to compensate inorganic carbon is physiologically significant, but may be ecologically less meaningful under most circumstances because of the normal abundance of carbon in sediment and water combined and because of its rapid replacement in natural systems via biological and physical-chemical processes.

#### Influence of Temperature on Distribution

56. Our results indicating broad thermal tolerance in *Myriophyllum*

are supported by the extensive latitudinal range reported for this species in North America (Holmquist 1971; Reed 1977; Aiken, Newroth, and Wile 1979). It occurs from Florida to the Arctic Circle. The ability of *Myriophyllum* to maintain considerable biomass under ice cover has been reported by Stanley et al. (1976), confirming its tolerance to low temperature.

57. A high thermal optimum for photosynthesis in *Myriophyllum* has been demonstrated by Stanley and Naylor (1972) and Titus and Adams (1979a). We determined lesser biomass in this species at the higher temperature levels, but must reiterate that productivity and biomass became increasingly unrelated at high temperatures because of greater biomass losses.

58. The turnover of biomass in *Myriophyllum* in lakes of the United States is extensive. For example, it has been estimated that two thirds or more of the production of this species senescences during the growing season along in Lake Wingra (Adams and McCracken 1974). From our data, it appears that turnover of biomass in *Myriophyllum* may increase somewhat with decreasing latitude in North America. This contention is supported by the data compiled by Grace and Wetzel (1978), indicating that both the seasonal maximum biomass of *Myriophyllum* and the time required for it to reach this maximum (inversely related to productivity) generally decrease from north to south in the United States. We suggest that this species in the United States generally occurs under thermal conditions conducive to both high productivity and high biomass loss. Thus, the ecological influence of *Myriophyllum* on lakes of the United States is potentially very great.

59. The distribution of *Egeria* in the United States has been described by Countryman (1970). It occurs sporadically in many states, but is most concentrated in the East and Southeast. Our data indicate that its growth is not greatly affected by temperature between 16° and 28°C, which implies that most of the United States and southern Canada may provide favorable thermal conditions for its existence. In the south, the growth of *Egeria* is likely restricted to the winter and spring months, since water temperatures above 28°C apparently promote its

decline. This contention is supported by the limited presence of *Egeria* in Florida as a whole and our own observations in Rodman Reservoir (north-central Florida) where this species completes its reproductive cycle in the early spring and is subsequently replaced by *Hydrilla*. The opposing thermal requirements of these two species may be an important consideration in their coexistence.

60. *Hydrilla* was first reported in the United States near Miami, Florida, in 1960 (Blackburn et al. 1969). Since that time, it has spread very rapidly throughout the southern states and has recently been reported in California (Yeo and McHenry 1977). Because of its rapid rate of growth, high reproductive capacity, and great competitive ability, *Hydrilla* has displaced the native vegetation in much of Florida.

61. Variations in the seasonal progression of growth with latitude have been reported for *Hydrilla* in Florida, where, on the basis of limited data, the productivity of this species appears to increase from north to south (Bowes, Holaday, and Haller 1979). The high thermal optimum and overall significance of temperature on the growth of this species are apparent in our data and in the studies of Van, Haller, and Bowes (1978) and Bowes, Holaday, and Haller (1979). These studies also indicate that tuber production, an important mode of reproduction, in this species is strongly influenced by temperature, with more tubers produced over a greater seasonal period at higher temperatures. From this information, we suggest that temperature may be the single most important factor limiting the growth and distribution of *Hydrilla* in North America. Its further encroachment into aquatic systems in this country should be significantly retarded with increasing latitude, but localized differences in water temperature (in industrial cooling ponds for instance) could contribute to discontinuities in its distribution.

#### Influence of Light on Distribution

62. Light appears to be much less important than temperature in influencing both the seasonal progression of biomass production and the geographical distribution of the species examined herein. The lesser

importance of light in these regards is a consequence of the extensive morphological and metabolic adaptability of these species to light over a broad range. However, light is probably the single most important factor determining the ability of these species to expand their depth distribution, particularly in eutrophic systems. In this regard, another important consideration is the degree to which stored nonstructural carbohydrates can support shoot growth in the spring (Titus and Adams 1979b). Obviously, an ability to commence shoot elongation at light levels inadequate to support net photosynthesis could promote an increase in depth distribution and may also confer a competitive advantage early in the growing season. This aspect of the depth distribution of submersed macrophytes deserves further investigation.

63. In our investigation, *Hydrilla* was most effective in increasing its shoot length. Notably at maximum shade, shoot elongation was quite extensive in spite of its minimal gain in biomass. Shoot elongation in *Egeria* and *Myriophyllum* was much less extensive than in *Hydrilla* at all shade levels. This suggests that *Hydrilla* may be relatively more effective in expanding its depth distribution than the other two species. *Hydrilla* has been observed by divers at depths in excess of 9 m in Lake Gatun, Panama, where it extends entirely to the water surface.\* The tremendous ability of this species to elongate unquestionably confers an advantage in systems of limited water transparency and may account for its ability to monopolize the entire surface area of many lakes in the southern United States. In contrast, *Myriophyllum* and *Egeria* are normally restricted to shallower regions of the littoral zone, particularly in systems of low water transparency.

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\* Personal communication, Nov 1979, H. E. Westerdahl, Research Ecologist, WES.

## PART V: CONCLUSIONS AND RECOMMENDATIONS

64. For many years, nutrition has been considered to be the primary determinant of the growth of aquatic macrophytes. Recently, however, it has become apparent that, in many eutrophic aquatic systems, environmental factors other than nutrients can assert equal or greater control over macrophyte growth. The results of this investigation clearly indicate that temperature substantially affects the productivity and distribution (both seasonal and geographical) in nature of the species considered herein. Because of the significant abilities of these species to concentrate their photoreceptive biomass at the water surface, light (in most circumstances) is probably less important than temperature in the production of these species, yet light does appear to be the primary determinant of their depth distribution.

65. Different macrophyte species demonstrate discrete ranges of thermal tolerance and optima for growth. For the most part, these differences are reflected in individual geographical distributions. Thus, a particular species promoting nuisance growth situations in one or several regions of the United States may not be a problem in others. For example, *Hydrilla verticillata* is very unlikely to be a problem in northern regions of the country because of its high thermal optimum for growth. For similar reasons, the peak standing biomass of *Myriophyllum spicatum* appears to decrease from north to south in the United States. *Egeria* apparently will not grow at temperatures much above 28°C, and thus should not be a problem during the summer in most parts of Florida.

66. As aquatic systems become shallower due to accumulations of inorganic sediment and organic matter, they provide an increasingly enhanced environment for colonization by macrophytes. In many systems, this process is accelerated by human activities in the watershed. For reasons that remain unclear, such systems are frequently susceptible to the invasion and subsequent explosive growth of introduced macrophyte species; the species considered in this investigation are foremost in importance in this regard among submersed species in the United States. Once such an invasion has been initiated, the strengths and weaknesses

of the native vegetation relative to those of the invading species will control the ultimate direction of plant succession (and species composition). The same situation can arise through the implementation of macrophyte control practices that disrupt competitive equilibria among species and consequently promote a resorting of species in accordance with an altered set of environmental conditions. Before the outcome of these vegetational changes can be predicted (and certainly before it can be manipulated), the role of major environmental factors promoting the growth of macrophytes needs to be specifically discerned. The results of this investigation should be carefully considered in the further development of aquatic plant management policies and related predictive capabilities.

## REFERENCES

- Adams, M. S., S. Guilizzoni, and S. Adams. 1978. Relationship of dissolved inorganic carbon to macrophyte photosynthesis in some Italian lakes. *Limnology and Oceanography* 23 (5):912-913.
- Adams, M. S., and M. D. McCracken. 1974. Seasonal production of the *Myriophyllum* component of the littoral of Lake Wingra, Wisconsin. *Journal of Ecology* 62:457-465.
- Adams, M. S., J. Titus, and M. D. McCracken. 1974. Depth distribution of photosynthetic activity in a *Myriophyllum spicatum* community in Lake Wingra. *Limnology and Oceanography* 19:377-389.
- Aiken, S. G., P. R. Newroth, and I. Wile. 1979. The biology of Canadian weeds. 34. *Myriophyllum spicatum* L. *Canadian Journal of Plant Science* 59:201-215.
- Allen, S. E., H. M. Grimshaw, J. A. Parkinson, and C. Quarmby. 1974. Chemical analysis of ecological materials. John Wiley and Sons, Inc., New York.
- Barko, J. W., P. G. Murphy, and R. G. Wetzel. 1977. An investigation of primary production and ecosystem metabolism in a Lake Michigan dune pond. *Archiv für Hydrobiologie*. 81:155-187.
- Barko, J. W., and R. M. Smart. 1979a. The nutritional ecology of *Cyperus esculentus*, an emergent aquatic plant, grown on different sediments. *Aquatic Botany* 6:13-28.
- Barko, J. W., and R. M. Smart. 1979b. The role of *Myriophyllum spicatum* in mobilization of sediment phosphorus. Pages 177-190 in J. R. Breck, R. T. Prentki, and O. L. Loucks, editors. *Aquatic plants, lake management and ecosystem consequences of lake harvesting*. Proceedings of Conference at Madison, Wisconsin, February 14-16, 1979.
- Barko, J. W., and R. M. Smart. 1980. Mobilization of sediment phosphorus by submersed freshwater macrophytes. *Freshwater Biology* 10: 229-238.
- Barko, J. W., and R. M. Smart. 1981. Sediment-based nutrition of submersed macrophytes (in press).
- Best, E. P. H., and J. T. Meulemans. 1979. Photosynthesis in relation to growth and dormancy in *Ceratophyllum demersum*. *Aquatic Botany* 6:53-65.
- Blackburn, R. D., L. W. Weldon, R. R. Yeo, and T. M. Taylor. 1969. Identification and distribution of similar appearing aquatic weeds in Florida. *Hyacinth Control Journal* 8:11-21.
- Bowes, G., A. S. Holaday, T. K. Van, and W. T. Haller. 1977a. Photosynthetic and photorespiratory carbon metabolism in aquatic plants. Pages 289-298 in *Proceedings of the Fourth International Congress on Photosynthesis*. Great Britain.

- Bowes, G., T. K. Van, L. A. Garrard, and W. T. Haller. 1977b. Adaptation to low light levels by *Hydrilla*. *Journal of Aquatic Plant Management* 15:32-35.
- Bowes, G., A. S. Holaday, and W. T. Haller. 1979. Seasonal variation in the biomass tuber density, and photosynthetic metabolism of hydrilla in three Florida lakes. *Journal of Aquatic Plant Management* 17:61-65.
- Boylen, C. W., and R. B. Sheldon. 1976. Submergent macrophytes: growth under winter ice cover. *Science* 194:841-842.
- Buscemi, P. A. 1958. Littoral oxygen depletion produced by a cover of *Elodea canadensis*. *Oikos* 9 (11):239-245.
- Carpenter, S. R., and M. S. Adams. 1977. The macrophyte tissue nutrient pool of a hardwater eutrophic lake: implications for macrophyte harvesting. *Aquatic Botany* 3:239-255.
- Countryman, W. D. 1970. The history, spread, and present distribution of some immigrant aquatic weeds in New England. *Hyacinth Control Journal* 8 (2):50-52.
- Dale, H. M., and T. J. Gillespie. 1977. The influence of submersed aquatic plants on temperature gradients in shallow water bodies. *Canadian Journal of Botany* 55:2216-2225.
- Denny, P. 1972. Sites of nutrient absorption in aquatic macrophytes. *Journal of Ecology* 60:819-829.
- Gerloff, G. C. 1975. Nutritional ecology of nuisance aquatic plants. National Environmental Research Center, Office of Research and Development, U. S. Environmental Protection Agency, Corvallis, Oreg.
- Gerloff, G. C., and P. H. Krombholz. 1966. Tissue analysis as a measure of nutrient availability for the growth of angiosperm aquatic plants. *Limnology and Oceanography* 11:529-537.
- Grace, J. B., and L. J. Tilly. 1976. Distribution and abundance of submerged macrophytes, including *Myriophyllum spicatum* L. (Angiospermae), in a reactor cooling reservoir. *Archiv für Hydrobiologie*. 77 4:475-487.
- Grace, J. B., and R. G. Wetzel. 1978. The production biology of Eurasian watermilfoil (*Myriophyllum spicatum* L.): A review. *Journal of Aquatic Plant Management* 16:1-11.
- Haag, R. W. 1979. The ecological significance of dormancy in some rooted aquatic plants. *Journal of Ecology* 67 (2):727-738.
- Haag, R. W., and P. R. Gorham. 1977. Effects of thermal effluent on standing crop and net production of *Elodea canadensis* and other submerged macrophytes in Lake Wabamun, Alberta. *Journal of Applied Ecology* 14:835-851.
- Haller, W. T., and D. L. Sutton. 1975. Community structure and competition between *Hydrilla* and *Vallisneria*. *Hyacinth Control Journal* 13:48-50.



- Holaday, A. S., and G. Bowes. 1980.  $C_4$  acid metabolism and dark  $CO_2$  fixation in a submersed macrophyte (*Hydrilla verticillata*). Plant Physiology 65:331-335.
- Holaday, S., W. T. Haller, and G. Bowes. 1977. Variations in the  $CO_2$  compensation point of aquatic plants. Plant Physiology, Supplement 59:65.
- Holmquist, C. 1971. Northerly localities for three aquatic plants, *Lemna triscula* L., *Ceratophyllum demersum* L., and *Myriophyllum spicatum* L. Botaniska Notiser 124 (3):335-342.
- Hough, R. A. 1979. Photosynthesis, respiration and organic carbon release in *Elodea canadensis* Michx. Aquatic Botany 7:1-11.
- Hough, R. A., and R. G. Wetzel. 1978. Photorespiration and  $CO_2$  compensation point in *Najas flexilis*. Limnology and Oceanography 23 (4):719-724.
- Hutchinson, G. E. 1975. A treatise of limnology. III. Aquatic macrophytes and attached algae. John Wiley and Sons, Inc., New York.
- Jana, S., and M. A. Choudhuri. 1979. Photosynthetic, photorespiratory and respiratory behavior of three submersed aquatic angiosperms. Aquatic Botany 7:13-19.
- Jupp, B. P., and D. H. N. Spence. 1977. Limitations on macrophytes in a eutrophic lake, Loch Leven. Journal of Ecology 65:175-186.
- Larcher, W. 1975. Physiological plant ecology. Springer-Verlag. New York.
- McNaughton, S. J. 1973. Comparative photosynthesis of Quebec and California ecotypes of *Typha latifolia*. Ecology 54:1260-1270.
- Osman, A. M., and F. L. Milthorpe. 1971. Photosynthesis of wheat leaves in relation to age, illuminance, and nutrient supply. II. Results. Photosynthetica 5:61-70.
- Peltier, W. H., and E. B. Welch. 1970. Factors affecting growth of rooted aquatic plants in a reservoir. Weed Science 18:7-9.
- Peverly, J. H. 1980. Elemental distribution and macrophyte growth downstream from an organic soil. Aquatic Botany 7:319-338.
- Phillips, G. L., D. Eminson, and B. Moss. 1978. A mechanism to account for macrophyte decline in progressively eutrophicated freshwaters. Aquatic Botany 4:103-126.
- Reed, C. F. 1977. History and distribution of Eurasian watermilfoil in United States and Canada. Phytologia 36:417-436.
- Rich, P. H., R. G. Wetzel, and N. V. Thuy. 1971. Distribution, production, and role of aquatic macrophytes in a southern Michigan marl lake. Freshwater Biology 1:3-21.

- Schmitt, M. R. 1977. The dependence of net photosynthesis on internal phosphorus levels in *Myriophyllum spicatum* L. Masters thesis. University of Wisconsin, Madison, Wisc.
- Sculthorpe, C. D. 1967. The biology of aquatic vascular plants. St. Martin's Press, New York.
- Sheldon, R. B., and C. W. Boylen. 1977. Maximum depth inhabited by aquatic vascular plants. *The American Midland Naturalist* 97 (1):248-254.
- Smith, W. E., N. E. Tolbert, and H. S. Ku. 1976. Variables affecting the CO<sub>2</sub> compensation point. *Plant Physiology* 58:143-146.
- Sondergaard, M. 1979. Light and dark respiration and the effect of the lacunal system on refixation of CO<sub>2</sub> in submerged aquatic plants. *Aquatic Botany* 6:269-283.
- Sondergaard, M., and R. G. Wetzel. 1980. Photorespiration and internal recycling of CO<sub>2</sub> in the submersed angiosperm *Scirpus subterminalis* Torr. *Canadian Journal of Botany* 58:591-598.
- Spence, D. H. N. 1967. Factors controlling the distribution of freshwater macrophytes, with particular reference to Scottish lochs. *Journal of Ecology* 55:147-170.
- Spence, D. H. N. 1972. Light on freshwater macrophytes. *Botanical Society of Edinburgh Transactions* 41:491-505.
- Spence, D. H. N. 1976. Light and plant response in freshwater. Pages 93-133 in G. C. Evans, R. Bainbridge, and O. Rockham, editors. *Light as an ecological factor: II*, 16th Symposium of the British Ecological Society, March 26-28, 1974.
- Spence, D. H. N., R. M. Campbell, and J. Chrystal. 1973. Specific leaf areas and zonation of freshwater macrophytes. *Journal of Ecology* 61:317-328.
- Spence, D. H. N., and J. Chrystal. 1970a. Photosynthesis and zonation of freshwater macrophytes. I. Depth distribution and shade tolerance. *New Phytologist* 69:205-215.
- Spence, D. H. N., and J. Chrystal. 1970b. Photosynthesis and zonation of freshwater macrophytes. II. Adaptability of species of deep and shallow water. *New Phytologist* 69:217-227.
- Spence, D. H. N., and H. M. Dale. 1978. Variations in the shallow water form of *Potamogeton richardsonii* induced by some environmental factors. *Freshwater Biology* 8:251-268.
- Stanley, R. A. 1970. Studies on nutrition, photosynthesis and respiration in *Myriophyllum spicatum* L. Doctoral dissertation. Duke University, Durham, N. C.
- Stanley, R. A., and A. W. Naylor. 1972. Photosynthesis in Eurasian watermilfoil (*Myriophyllum spicatum* L.). *Plant Physiology* 50:149-151.

- Stanley, R. A., E. Shackelford, D. Wade, and C. Warren. 1976. Effects of season and water depth on Eurasian watermilfoil. *Journal of Aquatic Plant Management* 14:32-36.
- Steemann Nielsen, E. 1947. Photosynthesis of aquatic plants with special reference to the carbon sources. *Dansk Botanisk Arkiv*. 12:5-71.
- Titus, J. E. 1977. The comparative physiological ecology of three submersed macrophytes. Doctoral dissertation. University of Wisconsin, Madison, Wisc.
- Titus, J. E., and M. S. Adams. 1979a. Coexistence and the comparative light relations of the submersed macrophytes *Myriophyllum spicatum* L. and *Vallisneria americana* Michx. *Oecologia* 40:273-286.
- Titus, J. E., and M. S. Adams. 1979b. Comparative carbohydrate storage and utilization patterns in the submersed macrophytes *Myriophyllum spicatum* L. and *Vallisneria americana* Michx. *American Midland Naturalist* 102:263-272.
- Van, T. K., W. T. Haller, and G. Bowes. 1976. Comparison of the photosynthetic characteristics of three submersed aquatic plants. *Plant Physiology* 58:761-768.
- Van, T. K., W. T. Haller, and L. A. Garrard. 1978. The effect of daylight and temperature on *Hydrilla* growth and tuber production. *Journal of Aquatic Plant Management* 16:57-59.
- Wetzel, R. G. 1975. *Limnology*. W. B. Saunders Company, Philadelphia, Penn.
- Wilson, D., and J. P. Cooper. 1969. Apparent photosynthesis and leaf characters in relation to leaf position and age, among contrasting *Lolium* genotypes. *New Phytologist* 68:645-655.
- Wiginton, J. R., and C. McMillan. 1979. Chlorophyll composition under controlled light conditions as related to the distribution of seagrasses in Texas and the U. S. Virgin Islands. *Aquatic Botany* 6:171-184.
- Yeo, R. R., and W. B. McHenry. 1977. *Hydrilla*, a new noxious aquatic weed in California. *California Agriculture* 31 (10):4-5.
- Young, C. A. 1973. The effects of temperature and other environmental factors on standing crop and phenological development of *Myriophyllum spicatum*. Masters thesis. University of Tennessee, Knoxville, Tenn.

In accordance with letter from DAEN-RDC, DAEN-ASI dated 22 July 1977, Subject: Facsimile Catalog Cards for Laboratory Technical Publications, a facsimile catalog card in Library of Congress MARC format is reproduced below.

Barko, John W

Growth and metabolism of three introduced submersed plant species in relation to the influences of temperature and light / by John W. Barko ... [et al.]. Vicksburg, Miss. : U. S. Waterways Experiment Station ; Springfield, Va. : available from National Technical Information Service, 1980.

46 p. : ill. ; 27 cm. (Technical report - U. S. Army Engineer Waterways Experiment Station ; A-80-1)

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References: p. 42-46.

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